

ON THE EXISTENCE OF ACCESSIBLE PATHS IN VARIOUS MODELS OF FITNESS LANDSCAPES

PETER HEGARTY AND ANDERS MARTINSSON

ABSTRACT. We present rigorous mathematical analyses of a number of well-known mathematical models for genetic mutations. In these models, the genome is represented by a vertex of the n -dimensional binary hypercube, for some n , a mutation involves the flipping of a single bit, and each vertex is assigned a real number, called its fitness, according to some rules. Our main concern is with the issue of existence of accessible paths, that is, monotonic paths across the hypercube along which fitness is always increasing. Our main results resolve open questions about three such models, which in the biophysics literature are known as House of Cards (HoC), Constrained House of Cards (CHoC) and Rough Mount Fuji (RMF). We prove that the probability of there being at least one (selectively) accessible path tends respectively to 0, 1 and 1, as n tends to infinity. A crucial idea is the introduction of a generalisation of the CHoC model, in which the fitness of the all-zeroes node is set to some $\alpha = \alpha_n \in [0,1]$. We prove that there is a very sharp threshold at $\alpha_n = \frac{\ln n}{n}$ for the existence of accessible paths. As a corollary we prove significant concentration, for α below the threshold, of the number of accessible paths about the expected value (the precise statement is technical, see Corollary 1.4). In the case of RMF, we prove that the probability of accessible paths existing tends to 1 provided the drift parameter $\theta = \theta_n$ satisfies $n\theta_n \rightarrow \infty$, and for any fitness distribution which is continuous on its support and whose support is connected.

0. NOTATION

Let $g, h : \mathbb{N} \rightarrow \mathbb{R}_+$ be any two functions. We will employ the following notations throughout, all of which are quite standard:

- (i) $g(n) \sim h(n)$ means that $\lim_{n \rightarrow \infty} \frac{g(n)}{h(n)} = 1$.
- (ii) $g(n) \lesssim h(n)$ means that $\limsup_{n \rightarrow \infty} \frac{g(n)}{h(n)} \leq 1$.
- (iii) $g(n) \gtrsim h(n)$ means that $h(n) \lesssim g(n)$.
- (iv) $g(n) = O(h(n))$ means that $\limsup_{n \rightarrow \infty} \frac{g(n)}{h(n)} < \infty$.
- (v) $g(n) = \Omega(h(n))$ means that $h(n) = O(g(n))$.
- (vi) $g(n) = \Theta(h(n))$ means that both $g(n) = O(h(n))$ and $h(n) = O(g(n))$ hold.
- (vii) $g(n) = o(h(n))$ means that $\lim_{n \rightarrow \infty} \frac{g(n)}{h(n)} = 0$.

If g, h are instead random variables, we use the above notations when the corresponding relationships hold with probability tending to 1 as $n \rightarrow \infty$. More precisely, $f(n) \sim g(n)$ for example means that, for all $\varepsilon_1, \varepsilon_2 > 0$ and $n \gg 0$,

$$(0.1) \quad \mathbb{P} \left(1 - \varepsilon_1 < \frac{f(n)}{g(n)} < 1 + \varepsilon_1 \right) > 1 - \varepsilon_2.$$

1. INTRODUCTION

In many basic mathematical models of genetic mutations, the genome is represented as a node of the n -dimensional binary hypercube \mathbb{Q}_n and each mutation involves the flipping of a single bit, hence displacement along an edge of \mathbb{Q}_n . Each node $v \in \mathbb{Q}_n$ is assigned a real number $f(v)$, called its *fitness*. The fitness of a node is not a constant, but is drawn from some probability distribution specified by the model. This distribution may vary from node to node in more or less complicated ways, depending on the model. Basically, however, evolution is considered as

Date: October 31, 2012.

2000 Mathematics Subject Classification. 60C05, 92D15 (primary); 05A05 (secondary).

favoring mutational pathways which, on average, lead to higher fitness. A fundamental concept in this regard is the following (see [W2], [W1], [FKVK]):

Definition 1.1. Let $f : \mathbb{Q}_n \rightarrow \mathbb{Q}_n$ be a fitness function. A (*selectively*) *accessible path* is a path in \mathbb{Q}_n

$$(1.1) \quad v_0 \rightarrow v_1 \rightarrow \cdots \rightarrow v_{n-1} \rightarrow v_n,$$

such that

- (i) v_0 and v_n are a pair of antipodal nodes,
- (ii) $f(v_i) > f(v_{i-1})$ for $i = 1, \dots, n$.

A basic question in such models is whether accessible paths exist or not with high probability. We shall be concerned below with the following three well-known models, in which no rigorous answer to this question has previously been given. Let $\mathbf{v}^0 = (0, 0, \dots, 0)$, $\mathbf{v}^1 = (1, 1, \dots, 1)$ denote the all-zeroes and all-ones vertices in \mathbb{Q}_n respectively.

MODEL 1: UNCONSTRAINED HOUSE OF CARDS (HoC)

This model is originally attributed to Kingman [Ki]. In the form we consider below, it was first studied by Kauffmann and Levin [KL]. We set $f(\mathbf{v}^1) := 1$ and, for every other node $v \in \mathbb{Q}_n$, let $f(v) \sim U(0, 1)$, the uniform distribution on the interval $[0, 1]$.

MODEL 2: CONSTRAINED HOUSE OF CARDS (CHoC)

This variant seems to have been considered only more recently, see for example [Klo] and [CH]. The only difference from MODEL 1 is that we fix $f(\mathbf{v}^0) := 0$.

MODEL 3: ROUGH MOUNT FUJI (RMF)

This model was first proposed in [A], see also [FWK]. It includes two parameters, a fixed probability distribution η , and a positive number θ , called the *drift*, which may depend on the dimension n . For each $v \in \mathbb{Q}_n$ one lets

$$(1.2) \quad f(v) = \theta \cdot d(v, \mathbf{v}^0) + \eta(v).$$

In other words, one first assigns a fitness to each node at random, according to η , and independent of all other nodes. Then the fitness of each node is shifted upwards by a fixed multiple of the Hamming distance from \mathbf{v}^0 .

In all three models, the basic random variable of interest is the number $X = X(n)$ of accessible paths from \mathbf{v}^0 to \mathbf{v}^1 . One thinks of \mathbf{v}^0 as the starting point of some evolutionary process, and \mathbf{v}^1 as the desirable endpoint. The HoC model is often referred to as a “null model” for evolution, since the fitnesses of all nodes other than \mathbf{v}^1 are assigned at random and independently of one another. No mechanism is prescribed which might push an evolutionary process in any particular direction. The CHoC model is not much better, though it does specify that the starting point is a global fitness minimum. The RMF model is a very natural, and simple, way to introduce an “arrow of evolution”, since the drift factor implies that successive $0 \rightarrow 1$ mutations will tend to increase fitness.

It seems intuitively obvious that the number X of accessible paths should, on average, be much higher in RMF than in HoC. One should be a little careful here, since in RMF, the node \mathbf{v}^1 is not assumed to be a global fitness maximum. Nevertheless, simulations reported in the biophysics literature support this intuition. In particular, let $P = P(n)$ be the probability of there being at least one accessible path, i.e.: $P = \mathbb{P}(X > 0)$. In [FKVK] it was conjectured explicitly that $P \rightarrow 0$ in the HoC model, and that $P \rightarrow 1$ in the RMF model, when η is

a normal distribution and θ is any positive constant. It also seems intuitively clear that the CHoC model lies somewhere in between. In [CH] this model was simulated for $n \leq 13$, and the authors conjecture, if somewhat implicitly, that P is monotonic decreasing in n and approaches a limiting value close to 0.7. In [FKVK], simulations were continued up to $n = 19$ and these indicated clearly that P was not, after all, monotonic decreasing. The authors abstain from making any explicit conjecture about the limiting behaviour of P .

Our main results below resolve all these issues. A crucial idea is to consider the following slight generalisation of the CHoC model:

MODEL 4: α -CONSTRAINED HOUSE OF CARDS (α -HoC)

Let $\alpha \in [0, 1]$. In this model, fitnesses are assigned as in the CHoC model, with the exception that we set $f(\mathbf{v}^0) := \alpha$. Hence, CHoC is the case $\alpha = 0$.

Let $P(n, \alpha)$ denote the probability of there being an accessible path in the α -constrained HoC model on the n -hypercube. Note that $P(n, \alpha)$ decreases as α increases. Our first main result is the following:

Theorem 1.2. *Let $\varepsilon = \varepsilon_n > 0$. If $n\varepsilon_n \rightarrow \infty$ then*

$$(1.3) \quad \lim_{n \rightarrow \infty} P\left(n, \frac{\ln n}{n} - \varepsilon_n\right) = 1$$

and

$$(1.4) \quad \lim_{n \rightarrow \infty} P\left(n, \frac{\ln n}{n} + \varepsilon_n\right) = 0.$$

It follows immediately that $P \rightarrow 1$ in the CHoC model. The above result says a lot more, however. It shows that there is a very sharp threshold at $\alpha = \alpha_n = \frac{\ln n}{n}$ for the existence of accessible paths in the α -HoC model. Theorem 1.2 will be proven in Section 2. We have the following immediate corollary for HoC:

Corollary 1.3. *Let X denote the number of accessible paths in the unconstrained House of Cards (HoC) model. Then*

$$(1.5) \quad \mathbb{P}(X > 0) \sim \frac{\ln n}{n}.$$

Proof. As $P(n, \alpha)$ is decreasing in α we know that for any $\alpha \in [0, 1]$, $\mathbb{P}(X > 0) \geq \alpha P(n, \alpha)$. Picking $\alpha = \frac{\ln n}{n} - \varepsilon_n$ where $n\varepsilon_n$ tends to infinity sufficiently slowly yields $\mathbb{P}(X > 0) \gtrsim \frac{\ln n}{n}$.

To get the upper bound, let $\alpha = \frac{\ln n}{n}$. Now, if the hypercube has accessible paths, then either \mathbf{v}^0 has fitness at most α or there is an accessible path where all nodes involved have fitness at least α . Obviously the former event occurs with probability α . Concerning the latter, if

$$(1.6) \quad \mathbf{v}^0 \rightarrow v_1 \rightarrow \cdots \rightarrow v_{n-1} \rightarrow \mathbf{v}^1$$

is any path, then the probability of all nodes along it having fitness at least α is $(1 - \alpha)^n$. The probability of fitness being increasing along the path is $1/n!$. Since there are $n!$ possible paths of the form (1.6), it follows from a simple union bound that

$$(1.7) \quad \mathbb{P}(X > 0) \leq \alpha + n! \frac{(1 - \alpha)^n}{n!} \leq \frac{\ln n}{n} + \frac{1}{n}.$$

■

Another Corollary of Theorem 1.2 concerns the distribution of the number of accessible paths in the α -HoC for $\alpha = \frac{\ln n}{n} - \varepsilon_n$ where $n\varepsilon_n \rightarrow \infty$. It is straightforward to show that the expected number of paths in the α -HoC model is $n(1 - \alpha)^{n-1}$ (see Proposition 2.1), which for this choice of α is $\sim e^{n\varepsilon_n}$. We have the following result:

Corollary 1.4. *Let X denote the number of accessible paths in the α -constrained House of Cards (α -HoC) model for $\alpha = \frac{\ln n}{n} - \varepsilon_n$ where $n\varepsilon_n \rightarrow \infty$. If $w_n \rightarrow \infty$ then*

$$(1.8) \quad \lim_{n \rightarrow \infty} \mathbb{P} \left(\frac{1}{w_n} \mathbb{E}[X] \leq X \leq w_n \mathbb{E}[X] \right) = 1.$$

Corollary 1.4 will be proven in Subsection 2.5.

Our second main result concerns the RMF model. For any function $f : \mathbb{R} \rightarrow \mathbb{R}$, recall that the *support* of f , denoted $\text{Supp}(f)$, is the set of points at which f is non-zero¹, i.e.: $\text{Supp}(f) = \{x : f(x) \neq 0\}$. We say that f has *connected support* if $\text{Supp}(f)$ is a connected subset of \mathbb{R} . Our result is the following:

Theorem 1.5. *Let η be any probability distribution whose p.d.f. is continuous on its support and whose support is connected. Let θ_n be any strictly positive function of n such that $n\theta_n \rightarrow \infty$ as $n \rightarrow \infty$. Then in the model (1.2), $P(n)$ tends to one as $n \rightarrow \infty$.*

This result is proven in Section 3. The proof follows similar lines to that of Theorem 1.2, but the analysis is somewhat simpler.

2. RESULTS FOR THE HO C MODELS

In this section, a path will always refer to a path through the directed hypercube, meaning that $d(v_i, \mathbf{v}^0)$ is strictly increasing along paths. For each path i from \mathbf{v}^0 to \mathbf{v}^1 let X_i be the indicator function of the event that i is accessible, and let $X = \sum_i X_i$ denote the number of accessible paths from \mathbf{v}^0 to \mathbf{v}^1 . Furthermore, given a path i from \mathbf{v}^0 to \mathbf{v}^1 in the n -dimensional hypercube, let $T(n, k)$ denote the number of paths from \mathbf{v}^0 to \mathbf{v}^1 that intersect i in exactly $k - 1$ interior nodes.

Proposition 2.1. *Let X denote the number of accessible paths in the α -HoC model. Then*

$$(2.1) \quad \mathbb{E}[X] = n(1 - \alpha)^{n-1}.$$

Proof. There are $n!$ paths through the hypercube. A path is accessible if all $n - 1$ interior nodes have fitness at least α and the fitness of the interior nodes is increasing along the path. This occurs with probability $(1 - \alpha)^{n-1} / (n - 1)!$. ■

Note that for $\alpha = \frac{\ln n}{n} + \varepsilon_n$, this implies that the probability of accessible paths tends to 0 for any sequence ε_n satisfying $n\varepsilon_n \rightarrow \infty$. Furthermore, for $\alpha = \frac{\ln n}{n} - \varepsilon_n$ where $n\varepsilon_n \rightarrow \infty$, the expected number of paths tends to infinity. To show that the probability of there being at least one accessible path tends to 1 in this case, we will begin by showing that the probability is at least $\frac{1}{4} - o(1)$ by estimating the second moment of X and applying Lemma 2.2. We will then use a symmetry argument to show that the probability must tend to 1.

Lemma 2.2. *Let X be a random variable with finite expected value and finite and non-zero second moment. Then*

$$(2.2) \quad \mathbb{P}(X \neq 0) \geq \frac{\mathbb{E}[X]^2}{\mathbb{E}[X^2]}.$$

Proof. Let $1_{X \neq 0}$ denote the indicator function of $X \neq 0$. Then, by the Cauchy-Schwartz inequality, $\mathbb{E}[X]^2 = \mathbb{E}[1_{X \neq 0} X]^2 \leq \mathbb{E}[1_{X \neq 0}^2] \cdot \mathbb{E}[X^2] = \mathbb{P}(X \neq 0) \cdot \mathbb{E}[X^2]$. ■

See also Exercise 4.8.1 in [AS].

¹Sometimes in the mathematical literature, the support of a function is defined to be the closure of this set.

Proposition 2.3. *Let i and j be paths with exactly $k - 1$ common interior nodes. Then*

$$(2.3) \quad \mathbb{E}[X_i X_j] \leq \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!},$$

where equality holds if the nodes where i and j differ are consecutive along the paths, i.e. if i and j diverges at most once. Furthermore,

$$(2.4) \quad \mathbb{E}[X^2] \leq \sum_{k=1}^n n! T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!}.$$

Proof. The event that i and j are both accessible occurs if all $2n - k - 1$ interior nodes have fitness at least α and the fitness of the interior nodes are ordered in such a way that fitness increases along both paths.

Conditioned on the event that all interior nodes have fitness at least α , all possible ways the fitness of the the interior nodes can be ordered are equally likely. This implies that the probability that both paths are accessible is $(1 - \alpha)^{2n-k-1} / (2n - k - 1)!$ times the number of ways to order the fitness of the interior nodes such that fitness increases along both paths.

To count the number of ways this can be done we color the numbers $1, \dots, 2n - k - 1$ in the following way: The number l is colored gray if the interior node with the l :th smallest fitness is contained in both paths, red if it is only contained in i and blue if only in j . Note that i and j uniquely determines which numbers must be gray for a valid ordering, and that given any coloring corresponding to a valid order one can recover the order.

Clearly, any coloring corresponding to a valid order colors half of the non-gray numbers red and half blue, which implies that there can be at most $\binom{2n-2k}{n-k}$ such orders. Furthermore, if i and j diverge at most once, one can always construct a valid order from such a coloring, so in this case there are exactly $\binom{2n-2k}{n-k}$ such orders.

As the number of ordered pairs of paths that intersect in exactly $k - 1$ interior nodes is $n! T(n, k)$, (2.4) follows from this estimate. ■

Remark 2.4. The numbers $T(n, k)$ already appear in the mathematical literature. The usual terminology is that $T(n, k)$ is the number of permutations of $\{1, 2, \dots, n\}$ with k *components*. An alternative terminology is that it is the number of permutations of $\{1, 2, \dots, n\}$ with $k - 1$ *global descents*. A global descent in a permutation $\pi_1 \pi_2 \dots \pi_n$ of $\{1, 2, \dots, n\}$ is a number $t \in [1, n - 1]$ such that $\pi_i > \pi_j$ for all $i \leq t$ and $j > t$. There is a simple 1 - 1 correspondence between permutations with k components and those with $k - 1$ global descents got by reading a permutation backwards. In other words, $\pi_1 \pi_2 \dots \pi_n$ has $k - 1$ global descents if and only if $\pi_n \pi_{n-1} \dots \pi_1$ has k components.

There is a database of the numbers $T(n, k)$ for small n and k , see [O2]. The book of Comtet [Co2] referred to at this link contains a couple of exercises and an implicit recursion formula for $T(n, k)$. Comtet has also performed a detailed asymptotic analysis of the numbers $T(n, 1)$ in [Co1]. Permutations with one component (i.e.: no global descents) are variously referred to as *connected*, *indecomposable*, *irreducible*. These seem to crop up quite a lot, see [O1]. However, estimates of the numbers $T(n, k)$ for general n and k like those in Propositions 2.10 and 2.12 below do not appear to have been obtained before.

2.1. Useful formulas for $T(n, k)$.

Proposition 2.5. *$T(n, 1)$ is uniquely defined by*

$$(2.5) \quad n! = \sum_{k=1}^n T(k, 1) (n - k)!.$$

Proof. Given a path i through the n -hypercube, the number of paths j that intersect i for the first time in step k is $T(k, 1) (n - k)!$. As any path through the hypercube intersects i for the first time after between 1 and n steps, the Proposition follows. ■

Proposition 2.6.

$$(2.6) \quad n! \left(1 - O\left(\frac{1}{n}\right) \right) \leq T(n, 1) \leq n!$$

Proof. By definition, $T(n, 1) \leq n!$. Using this, Proposition 2.5 implies that $T(n, 1)$ is at least $n! - \sum_{k=1}^{n-1} k!(n-k)! = n! - O((n-1)!)$. ■

Proposition 2.7.

$$(2.7) \quad T(n, k) = \sum_{\substack{s_1, \dots, s_k \geq 1 \\ s_1 + \dots + s_k = n}} T(s_1, 1) \cdot \dots \cdot T(s_k, 1)$$

Proof. Given a path i , the number of paths that intersect i for the first time after s_1 steps, for the second time after s_2 more steps and so on up to the last time (at $11 \dots 1$) after n steps is $T(s_1, 1) \cdot \dots \cdot T(s_{k-1}, 1) \cdot T(n - s_1 - \dots - s_{k-1}, 1)$. Let $s_k = n - s_1 - \dots - s_{k-1}$. $T(n, k)$ is obtained by summing over all possible values of s_1, \dots, s_k . ■

Proposition 2.8. For $k \geq 2$, $T(n, k)$ satisfies

$$(2.8) \quad T(n, k) = \sum_{s=1}^{n-k+1} T(s, 1) T(n-s, k-1).$$

Proof. It follows by induction that this sum equals the right hand side in (2.7). ■

2.2. Upper bounds for $T(n, k)$.

Proposition 2.9. For any $n \geq k \geq 1$

$$(2.9) \quad T(n, k) \leq k \sum \left((n - \sum_j s_j)! \prod_j s_j! \right)$$

where the first sum goes over all integers s_1, \dots, s_{k-1} such that $s_j \geq 1$ for all j and $\max_j s_j \leq n - \sum_j s_j$.

Proof. Consider the formula for $T(n, k)$ in Proposition 2.7. By symmetry, $T(n, k)$ is at most k times contribution from terms where $s_j \leq s_k$ for $j = 1, \dots, k-1$. The Proposition follows by applying $T(s, 1) \leq s!$. ■

Proposition 2.10. There is a positive constant c such that for all $n \geq k \geq 1$

$$(2.10) \quad T(n, k) \leq k(n-k+1)! e^{c(k-1)/(n-k+1)}.$$

Proof. We use Proposition 2.9 and make the following approximations:

- substitute $(n - \sum_j s_j)!$ by $\beta^{n - \sum_j s_j}$ where $\beta = ((n-k+1)!)^{1/(n-k+1)}$. It follows from log-convexity of $l!$ that $\beta^l \geq l!$ for any $0 \leq l \leq n-k+1$.
- let all s_j go from 1 to $\lfloor (n-k+1)/2 + 1 \rfloor$.

This yields

$$(2.11) \quad T(n, k) \leq k(n-k+1)! \left(\sum_{s=1}^{\lfloor (n-k+1)/2 + 1 \rfloor} s! \beta^{1-s} \right)^{k-1}.$$

We now claim that this sum is always less than $1 + c/(n - k + 1)$ for sufficiently large c . Indeed

$$\begin{aligned}
\sum_{s=1}^{\lfloor (n-k+1)/2+1 \rfloor} s! \beta^{1-s} &= 1 + 2\beta^{-1} + \beta^{-1} \sum_{t=1}^{\lfloor (n-k+1)/2-1 \rfloor} t!(t+1)(t+2)\beta^{-t} \\
&\leq 1 + 2\beta^{-1} + \\
&\quad + e\beta^{-1} \sum_{t=1}^{\lfloor (n-k+1)/2-1 \rfloor} \sqrt{t}(t+1)(t+2) \left(\frac{n-k+1}{2e}\right)^t \left(\frac{n-k+1}{e}\right)^{-t} \\
&\leq 1 + 2\beta^{-1} + e\beta^{-1} \sum_{t=1}^{\infty} \sqrt{t}(t+1)(t+2)2^{-t} \\
&\leq 1 + c(n-k+1)^{-1}.
\end{aligned}$$

Here we have used that $(n-k+1)/e \leq \beta \leq (n-k+1)$ and that $n! \leq en^{n+1/2}e^{-n}$, which follows from standard estimates of factorials.

The Proposition now follows from this result together with (2.11). ■

Proposition 2.11. *For any fixed l there is a constant $C_l > 0$ such that*

$$(2.12) \quad T(n, n-l) \leq C_l n^l$$

for all $n \geq 1$.

Proof. We may, without loss of generality, assume that $n \geq 2l$.

Recall the formula for $T(n, n-l)$ in Proposition 2.7. As $s_1, \dots, s_{n-l} \geq 1$ and $s_1 + \dots + s_{n-l} = n$ it is easy to see that all but at most l variables are 1. This implies that $T(n, n-l)$ is at most $\binom{n-l}{l}$ times the contribution from all terms where $s_{l+1} = \dots = s_{n-l} = 1$. Using $T(1, 1) = 1$, we get

$$(2.13) \quad T(n, n-l) \leq \binom{n-l}{l} \sum_{\substack{s_1, \dots, s_l \geq 1 \\ s_1 + \dots + s_l = 2l}} T(s_1, 1) \cdot \dots \cdot T(s_l, 1) \leq C_l n^l.$$

■

Proposition 2.12. *For sufficiently large c*

$$(2.14) \quad T(n, n-l) \leq c(l+1) \left(\frac{n+2l}{5}\right)^l.$$

Proof. Let

$$(2.15) \quad S(n, n-l) = (l+1) \left(\frac{n+2l}{5}\right)^l$$

i.e.

$$(2.16) \quad S(n, k) = (n-k+1) \left(\frac{3n-2k}{5}\right)^{n-k}.$$

We will begin by showing that $S(n, k)$ satisfies

$$(2.17) \quad S(n, k) \geq \sum_{i=1}^{n-k+1} i! S(n-i, k-1)$$

for $k > 1$ and sufficiently large $n - k$. Here we have

$$\begin{aligned}
\sum_{i=1}^{n-k+1} i! S(n-i, k-1) &= \sum_{i=1}^{n-k+1} i! (n-k+2-i) \left(\frac{3n-2k-3i+2}{5} \right)^{n-k-i+1} \\
&\leq (n-k+1) \left(\frac{3n-2k-1}{5} \right)^{n-k} + \\
&\quad + \sum_{i=2}^{n-k+1} i! (n-k+1) \left(\frac{3n-2k}{5} \right)^{n-k-i+1} \\
&= S(n, k) \left(\left(1 - \frac{1}{3n-2k} \right)^{n-k} + \sum_{i=2}^{n-k+1} i! \left(\frac{3n-2k}{5} \right)^{-i+1} \right),
\end{aligned}$$

where

$$\begin{aligned}
\left(1 - \frac{1}{3n-2k} \right)^{n-k} &\leq \exp \left(-\frac{n-k}{3n-2k} \right) \\
&\leq \exp \left(-\frac{n-k}{3n} \right) \\
&\leq \max \left(\frac{1}{2}, 1 - \frac{n-k}{6n} \right),
\end{aligned}$$

and

$$\begin{aligned}
&\sum_{i=2}^{n-k+1} i! \left(\frac{3n-2k}{5} \right)^{-i+1} \\
&\leq \frac{10}{3n-2k} + \frac{5}{3n-2k} \sum_{j=1}^{n-k-1} j! (j+1)(j+2) \left(\frac{3n-2k}{5} \right)^{-j} \\
&\leq \frac{10}{3n-2k} + \frac{5e}{3n-2k} \sum_{j=1}^{\infty} \sqrt{j} (j+1)(j+2) \left(\frac{n-k}{e} \right)^j \left(\frac{3n-2k}{5} \right)^{-j} \\
&\leq \frac{1}{n} \left(10 + 5e \sum_{j=1}^{\infty} \sqrt{j} (j+1)(j+2) \left(\frac{5}{3e} \right)^j \right) \\
&= \frac{C}{n}.
\end{aligned}$$

It follows directly that (2.17) holds for $k > 1$ and $n - k \geq 6C$.

Now, if we can choose c so that $T(n, k) \leq cS(n, k)$ for $k = 1$ and for $n - k < 6C$ the Proposition follows from Proposition 2.8 by induction on k . Hence it suffices to show the Proposition for these two cases.

For $k = 1$, the inequality holds for sufficiently large c by the fact that

$$\begin{aligned}
\frac{T(n, 1)}{S(n, 1)} &\leq \frac{n!}{n \left(\frac{3n-2}{5} \right)^{n-1}} \\
&\leq e\sqrt{n} \left(\frac{n}{e} \right)^n \frac{1}{n \left(\frac{3n-2}{5} \right)^{n-1}} \\
&= \frac{3e}{5} \sqrt{n} \left(\frac{5}{3e} \right)^n \left(1 - \frac{2}{3n} \right)^{-n+1} \\
&\rightarrow 0 \text{ as } n \rightarrow \infty.
\end{aligned}$$

For $n - k < 6C$, this follows from Proposition 2.11. ■

2.3. Computing $\mathbb{E}[X^2]$. Pick $\delta > 0$ sufficiently small. We divide the sum in (2.4) into the contribution from $k \leq (1 - \delta)n$ and the contribution from $k > (1 - \delta)n$.

$$(2.18) \quad \sum_{k=1}^n n!T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!} \\ = \sum_{k=1}^{(1-\delta)n} n!T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!} + \sum_{l=0}^{\delta n} n!T(n, n-l) \frac{\binom{2l}{l} (1-\alpha)^{n+l-1}}{(n+l-1)!}$$

Proposition 2.13. *For k constant and $\alpha = o(1)$*

$$(2.19) \quad n!T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!} \sim k 2^{1-k} n^2 (1-\alpha)^{2n}.$$

Proof. A simple lower bound on $T(n, k)$ is the number of permutations with k components where all but one component contains exactly 1 element. For sufficiently large n this is given by $kT(n-k+1, 1)$, which by Proposition 2.6 is $\sim k(n-k+1)!$. Furthermore, from Proposition 2.10 we know that $T(n, k)$ is most $(1 + o(1))k(n-k+1)!$. Hence for constant k , $T(n, k) \sim k(n-k+1)!$. The Proposition now follows from standard estimates of factorials. \blacksquare

Proposition 2.14. *Let $\alpha = o(1)$. For any $0 < \delta < 1$, the contribution to (2.18) from $k \leq (1 - \delta)n$ is $\sim 4n^2(1 - \alpha)^{2n}$.*

Proof. From Proposition 2.10 it follows that there is a constant C_δ such that $T(n, k) \leq C_\delta k(n-k+1)!$ whenever $k \leq (1 - \delta)n$. Using this we have

$$(2.20) \quad n!T(n, k) \frac{\binom{2n-2k}{n-k}}{(2n-k-1)!} \leq C_\delta n!k(n-k+1)! \frac{\binom{2n-2k}{n-k}}{(2n-k-1)!}$$

for all $k \leq (1 - \delta)n$. Now by extensive use of Stirling's formula there is a constant $C > 0$ such that:

$$C_\delta n!k(n-k+1)! \frac{\binom{2n-2k}{n-k}}{(2n-k-1)!} \\ \leq C_\delta Ck\sqrt{n} \left(\frac{n}{e}\right)^n \sqrt{n-k} \left(\frac{n-k}{e}\right)^{n-k} (n-k+1) \frac{4^{n-k} (2n-k)}{\sqrt{2n-k} \left(\frac{2n-k}{e}\right)^{2n-k}} \\ = C_\delta Ck(n-k+1)\sqrt{n(2n-k)} 2^{-k} \left(\left(1 - \frac{k}{n}\right)^{\frac{n}{k}-1} \left(1 - \frac{k}{2n}\right)^{-\frac{2n}{k}+1} \right)^k$$

where

$$\left(1 - \frac{k}{n}\right)^{\frac{n}{k}-1} \left(1 - \frac{k}{2n}\right)^{-\frac{2n}{k}+1} \leq \left(1 - \frac{k}{2n}\right)^{\frac{2n}{k}-2} \left(1 - \frac{k}{2n}\right)^{-\frac{2n}{k}+1} \\ = \left(1 - \frac{k}{2n}\right)^{-1} \\ \leq \left(1 - \frac{1-\delta}{2}\right)^{-1} \\ = \frac{2}{1+\delta}.$$

This means that for all $\delta > 0$ there exists a constant C'_δ such that for $k \leq (1 - \delta)n$ and sufficiently large n we have

$$(2.21) \quad n!T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!} \leq C'_\delta n^2 (1-\alpha)^{2n} k (1+\delta)^{-k} (1-\alpha)^{-k}.$$

Since $\sum k(1+\delta)^{-k}(1-\alpha)^{-k}$ converges for sufficiently small α we have shown that the contribution from $k \leq (1-\delta)n$ is $O(n^2(1-\alpha)^{2n})$. Furthermore, if we assume that n is sufficiently large so that $(1+\delta)(1-\alpha) \geq (1+\frac{\delta}{2})$, then as the terms in the sum

$$(2.22) \quad \sum_{k=1}^{(1-\delta)n} \frac{1}{n^2(1-\alpha)^{2n}} n! T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!}$$

are dominated by the terms in

$$(2.23) \quad \sum_{k=1}^{\infty} C'_\delta k \left(1 + \frac{\delta}{2}\right)^{-k}$$

which converges, it follows by dominated convergence together with Proposition 2.13 that

$$\sum_{k=1}^{(1-\delta)n} \frac{1}{n^2(1-\alpha)^{2n}} n! T(n, k) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!} \rightarrow \sum_{k=1}^{\infty} k 2^{1-k} = 4 \text{ as } n \rightarrow \infty.$$

■

Proposition 2.15. *For sufficiently small $\delta > 0$ and $\alpha = o(1)$, the contribution to (2.18) from $k > (1-\delta)n$ is $O(n(1-\alpha)^n)$.*

Proof. Using Proposition 2.12 there is a constant C such that this sum is bounded by

$$\begin{aligned} \sum_{l=0}^{\delta n} n! T(n, n-l) \frac{\binom{2l}{l} (1-\alpha)^{n+l-1}}{(n+l-1)!} &\leq C \sum_{l=0}^{\delta n} n! (l+1) \left(\frac{n+2l}{5}\right)^l \frac{\binom{2l}{l} (1-\alpha)^{n+l-1}}{(n+l-1)!} \\ &\leq C(1-\alpha)^{n-1} \sum_{l=0}^{\delta n} n^{1-l} (l+1) \left(\frac{n+2l}{5}\right)^l 4^l \\ &\leq Cn(1-\alpha)^{n-1} \sum_{l=0}^{\infty} (l+1) \left(\frac{4(1+2\delta)}{5}\right)^l \end{aligned}$$

where the last sum clearly converges for sufficiently small δ .

■

Proposition 2.16. *Let X be the number of accessible paths in the α -HoC model where $\alpha = \frac{\ln n}{n} - \varepsilon_n$ where $n\varepsilon_n \rightarrow \infty$. Then*

$$(2.24) \quad \mathbb{E}[X^2] \sim 4n^2(1-\alpha)^{2n}.$$

Proof. From Proposition 2.3 together with Propositions 2.14 and 2.15 we know that

$$(2.25) \quad \mathbb{E}[X^2] \leq (4 + o(1)) n^2(1-\alpha)^{2n} + O(n(1-\alpha)^n),$$

where one can show that $n(1-\alpha)^n = o(n^2(1-\alpha)^{2n})$, provided $n\varepsilon_n \rightarrow \infty$.

To derive a tight lower bound for $\mathbb{E}[X^2]$, consider the sum of $\mathbb{E}[X_i X_j]$ over all pairs of paths whose number of common interior nodes, $k-1$, is at most $\frac{n}{2}-1$ and that diverge at most once. Expressed in terms of components of permutations, for a fixed i and k , the number of paths j that satisfy this equals the number of permutations with k components, where all but one component contains exactly 1 element. This can clearly be done in $kT(n-k+1, 1) \sim k(n-k+1)!$ ways.

By Proposition 2.3 this yields

$$(2.26) \quad \mathbb{E}[X^2] \geq \sum_{k=1}^{n/2} n! k T(n-k+1, 1) \frac{\binom{2n-2k}{n-k} (1-\alpha)^{2n-k-1}}{(2n-k-1)!}.$$

Proceeding in a manner similar to the proof of Proposition 2.14, we get that

$$(2.27) \quad \sum_{k=1}^{n/2} n!kT(n-k+1, 1) \frac{\binom{2n-2k}{n-k}(1-\alpha)^{2n-k-1}}{(2n-k-1)!} \sim 4n^2(1-\alpha)^{2n}$$

which concludes the proof. \blacksquare

From this proof we can observe that almost all of the contribution to $\mathbb{E}[X^2]$ comes from pairs of paths we considered in the lower bound. This implies the following:

Corollary 2.17. *Assume $\alpha = \frac{\ln n}{n} - \varepsilon_n$ where $n\varepsilon_n \rightarrow \infty$. For any $0 < \delta < 1$, the contribution to $\mathbb{E}[X^2]$ from all pairs of paths that either share more than $(1-\delta)n$ common nodes or that diverge more than once is $o(n^2(1-\alpha)^{2n})$.*

2.4. Proof of Theorem 1.2. From Propositions 2.1 and 2.16 together with Lemma 2.2 it follows that, for any sequence ε_n satisfying $n\varepsilon_n \rightarrow \infty$,

$$(2.28) \quad \liminf_{n \rightarrow \infty} P\left(n, \frac{\ln n}{n} - \varepsilon_n\right) \geq \frac{1}{4}.$$

In the following Proposition, we will show that this result can be improved to any value less than one, implying that $P(n, \frac{\ln n}{n} - \varepsilon_n)$ must tend to 1.

Proposition 2.18. *Define the sequence C_k by $C_1 = \frac{1}{4}$ and $C_{k+1} = 1 - (1 - C_k)\left(1 - \frac{C_k}{2}\right)$ for $k \geq 1$. If $\alpha = \frac{\ln n}{n} - \varepsilon_n$ for some sequence ε_n satisfying $n\varepsilon_n \rightarrow \infty$, then for any k , $P(n, \alpha) \geq C_k - o(1)$.*

Proof. As noted above, the case $k = 1$ follows directly from Propositions 2.1 and 2.16 together with Lemma 2.2.

Assume the Proposition is true for k . By Chebyshev's inequality, there are, with probability $1 - o(1)$, two nodes, a_1, a_2 , satisfying $d(a_1, \mathbf{v}^0) = d(a_2, \mathbf{v}^0) = 1$ that have fitness at most $\varepsilon_n/3$, and two nodes, b_1, b_2 , satisfying $d(b_1, \mathbf{v}^1) = d(b_2, \mathbf{v}^1) = 1$ that have fitness at least $1 - \varepsilon_n/3$. We may without loss of generality assume that neither a_1 and b_1 nor a_2 and b_2 are antipodes. By assumption, the probability of accessible paths in the induced subgraph between a_1 and b_1 is at least $C_k - o(1)$. This means that the Proposition holds for $k+1$ if the probability of accessible paths passing through both a_2 and b_2 but no node on the induced subgraph between a_1 and b_1 is at least $\frac{C_k}{2} - o(1)$.

The criterion for a path to pass through the induced subgraph between a_1 and b_1 is that it must flip the bit that is 1 in a_1 before the 0 in b_1 . This means that at least half of the paths passing through a_2 and b_2 do not pass through a node on the induced subgraph between a_1 and b_1 . As the distribution of accessible paths is invariant under permutations of bits, the probability of accessible paths of this type is at least $\frac{C_k}{2} - o(1)$. The Proposition follows by induction. \blacksquare

2.5. Proof of Corollary 1.4. A key observation is that an alternative formulation of the α -HoC model is to assign fitnesses as in the CHoC model and then remove each node except \mathbf{v}^0 and \mathbf{v}^1 independently with probability α (a similar idea is used in Section 3). More precisely, if we consider the nodes in the α -HoC model removed if they have fitness less than α , then these two models yield the same distribution of fitnesses (up to an affine transformation). Similarly, assigning fitnesses as in the α -HoC model and then removing each node except \mathbf{v}^0 and \mathbf{v}^1 independently with probability δ is an equivalent formulation of the $(1 - (1 - \alpha)(1 - \delta))$ -HoC model.

The upper bound on X is simply Markov's inequality. We now turn to the lower bound. To simplify calculations we may, without loss of generality, assume that $w_n = o(n\varepsilon_n)$ and that $1 \leq w_n \leq e^{n\varepsilon_n}$ for all n . Let $\delta_n = \varepsilon_n - \frac{\ln w_n}{n}$ and let Y denote the number of intact accessible paths using the same assignment of fitnesses as for X but after removing each node except \mathbf{v}^0

and \mathbf{v}^1 independently with probability δ_n . By assumption, we know that $0 \leq \delta_n \leq \frac{\ln n}{n}$, so δ_n is always a valid probability.

By the reasoning above, Y has the same distribution as the number of accessible paths in the α'_n -HoC model where $\alpha'_n = (1 - (1 - \alpha)(1 - \delta_n)) = \frac{\ln n}{n} - \frac{o(1) + \ln w_n}{n}$. As $o(1) + \ln w_n \rightarrow \infty$ as $n \rightarrow \infty$ it follows from Theorem 1.2 that $\lim_{n \rightarrow \infty} \mathbb{P}(Y = 0) = 0$.

As accessible path has $n - 1$ interior nodes, the probability of an accessible path remaining intact after removing each interior node independently with probability δ_n is $(1 - \delta_n)^{n-1}$. Now, if all accessible paths before we remove any nodes have distinct interior nodes, we know that the probability of no accessible paths remaining is $(1 - (1 - \delta_n)^{n-1})^X$. If there are paths that share interior nodes, it is intuitively clear that the probability of no accessible paths remaining must be even higher. For a complete proof of this, see for instance Theorem 8.1.1 in [AS]. This implies that

$$(2.29) \quad \mathbb{P}(Y = 0 \mid X) \geq (1 - (1 - \delta_n)^{n-1})^X.$$

But since $\lim_{n \rightarrow \infty} \mathbb{P}(Y = 0) = 0$ and $(1 - (1 - \delta_n)^{n-1})^X = e^{-(1+o(1))e^{-n\delta_n}X}$ it follows that $e^{-n\delta_n}X$ must tend to infinity in probability. To conclude the proof we note that $e^{-n\delta_n}X = \frac{X}{e^{n\delta_n}/w_n} \sim \frac{X}{\mathbb{E}[X]/w_n}$.

Remark 2.19. Note that Proposition 2.16 implies that $\text{Var}(X) \sim 3\mathbb{E}[X]^2$ for α in this regime, so no significant improvement on Corollary 1.4 can be made by a naive application of Chebyshev's inequality.

3. RESULTS FOR THE RMF MODEL

Let $n \in \mathbb{N}$ and let $\varepsilon = \varepsilon_n$ be some strictly positive function. Consider the n -dimensional hypercube in which \mathbf{v}^0 and \mathbf{v}^1 are present, and where every other vertex is present with probability ε_n , independently of all other vertices. Let $Y = Y_{n,\varepsilon_n}$ denote the number of accessible paths from \mathbf{v}^0 to \mathbf{v}^1 , where in this model a path is accessible if Hamming distance from \mathbf{v}^0 is strictly increasing and all vertices along the path are present. The following proposition may be well-known, as it can be interpreted in the context of site percolation on the oriented hypercube. However, we were not able to locate a suitable reference.

Proposition 3.1. (i) $\mathbb{E}[Y] = n! \cdot \varepsilon_n^{n-1}$.

(ii) Let $n \rightarrow \infty$ and suppose that $n\varepsilon_n \rightarrow \infty$. Then $\text{Var}(Y) = o(\mathbb{E}[Y]^2)$, and hence

$$(3.1) \quad Y \sim \mathbb{E}[Y] \sim \frac{\sqrt{2\pi n}}{\varepsilon_n} \left(\frac{n\varepsilon_n}{e} \right)^n.$$

Proof. There are $n!$ possible paths in the n -hypercube. Each path contains $n - 1$ interior vertices, each of which is present with probability ε_n . This proves (i). Set $\mu = \mu_n := n!\varepsilon_n^{n-1}$. Now suppose $n\varepsilon_n \rightarrow \infty$. Let Y_i be the indicator of the event that the i :th increasing path is accessible, where the paths have been ordered in any way. Fix any path i_0 . Then, by a standard second moment estimate (see Section 2),

$$(3.2) \quad \text{Var}(Y) \leq \mu + n! \cdot \sum_{j \sim i_0} \mathbb{P}(Y_{i_0} \wedge Y_j),$$

where the sum is taken over all paths j which intersect the path i_0 in at least one interior vertex. Let k be the number of intersection points. This leaves $T(n, k + 1)$ possibilities for the path j . The paths i_0 and j contain a total of $2n - 2 - k$ different interior vertices, hence the probability of both being present is ε_n^{2n-2-k} . Hence

$$(3.3) \quad \text{Var}(Y) \leq \mu + n! \cdot \sum_{k=2}^n T(n, k) \varepsilon_n^{2n-1-k} \leq \mu + \mu^2 \cdot \sum_{k=2}^n \frac{T(n, k)}{n! \varepsilon_n^{k-1}}.$$

Hence, since $\mu \rightarrow \infty$ when $n\varepsilon_n \rightarrow \infty$, it suffices to show that

$$(3.4) \quad \sum_{k=2}^n \frac{T(n, k)}{n! \varepsilon_n^{k-1}} = o(1).$$

We now follow the same strategy as in Section 2, but the analysis here is much simpler. Let $\delta \in (0, 1)$. We divide the sum in (3.4) into two parts, one for $k < (1 - \delta)n$ and the other for $k \geq (1 - \delta)n$. From Proposition 2.10 and Lebesgue's dominated convergence theorem, it follows easily that, for any $\delta > 0$, the sum over terms $k < (1 - \delta)n$ is bounded by $(1 + o_n(1)) \sum_{k=2}^{\infty} \frac{k}{(n\varepsilon_n)^{k-1}} = O(\frac{1}{n\varepsilon_n}) = o(1)$, provided $n\varepsilon_n \rightarrow \infty$. Similarly, from Proposition 2.12 it follows that the sum over terms $k \geq (1 - \delta)n$ is bounded by

$$(3.5) \quad \frac{c}{\mu} \sum_{l=0}^{\delta n} (l+1) \left(\frac{1+2\delta}{5} \cdot n\varepsilon_n \right)^l,$$

where c is an absolute constant. Since $n\varepsilon_n \rightarrow \infty$, the sum in (3.5) is bounded by $1 + o(1)$ times the last term, and hence is $O((n\varepsilon_n)^{\delta n})$, which is in turn $o(\mu)$. This proves (3.4) and completes the proof of the proposition. \blacksquare

We now turn to the Rough Mount Fuji (RMF) model and prove Theorem 1.5.

We shall abuse notation and also use η to denote the p.d.f. of the probability distribution under consideration. So suppose η has connected support and is continuous there. Let $\delta > 0$ be given. Then there exists a bounded, closed interval $I = I_\delta \subseteq \text{Supp}(\eta)$ such that $\int_{I_\delta} \eta(x) dx > 1 - \delta$. The quantity $c_{\eta, \delta} = \min_{x \in I_\delta} \eta(x)$ exists, is non-zero and, obviously, depends only on η and δ . Now let $n \in \mathbb{N}$ and $\theta = \theta_n > 0$ be given. Without loss of generality, we may assume that the interval I_δ has length $l(I_\delta) > \theta_n/2$. By definition of I_δ , with probability at least $(1 - \delta)^2$ each of $\eta(\mathbf{v}^0)$ and $\eta(\mathbf{v}^1)$ lie in I_δ . Let X_{δ, n, θ_n} be the number of accessible paths in the n -hypercube, where fitnesses are assigned as in (1.2), and conditioning on the fact that both $\eta(\mathbf{v}^0)$ and $\eta(\mathbf{v}^1)$ lie in I_δ . We claim that, if n is sufficiently large, then X_{δ, n, θ_n} stochastically dominates the random variable Y_{n, ε_n} in Proposition 3.1, where $\varepsilon_n = c_{\eta, \delta} \cdot \frac{\theta_n}{2}$.

To see this, first note that, as long as $l(I_\delta) > \theta_n/2$ then, for any point $x \in I_\delta$, there will be an interval I_x of length at least $\theta_n/2$, which contains x and lies entirely within I_δ . By assumption, any such interval captures at least $c_{\eta, \delta} \cdot \frac{\theta_n}{2}$ of the distribution η . For any adjacent pair (v, v') of vertices in the hypercube such that $d(v', \mathbf{v}^0) = d(v, \mathbf{v}^0) + 1$, if $\eta(v') > \eta(v) - \theta_n$, then v' is accessible from v . Assuming $\eta(\mathbf{v}^0) \in I_\delta$, it follows that we can choose, for each layer i in the hypercube, an interval $I_i \subseteq I_\delta$ of length $\theta_n/2$ such that any path

$$(3.6) \quad \mathbf{v}^0 \rightarrow v_1 \rightarrow v_2 \cdots \rightarrow v_{n-1}$$

for which $\eta(v_i) \in I_i$ for all $i = 1, \dots, n-1$, is accessible. If n is sufficiently large, we can also ensure that the interval I_{n-1} contains $\eta(\mathbf{v}^1)$, so that any viable path (3.6) can definitely be continued to \mathbf{v}^1 . The stochastic domination of Y_{n, ε_n} by X_{δ, n, θ_n} now follows. Then one just needs to apply Proposition 3.1 and Theorem 1.5 follows immediately.

Remark 3.2. Suppose $\text{Supp}(\eta)$ is also bounded, and that θ is a constant, independent of n . Let

$$(3.7) \quad C_{\eta, \theta} := \min_{l(I)=\theta/2, I \subseteq \text{Supp}(\eta)} \int_I \eta(x) dx,$$

where I denotes a closed interval. Then this minimum exists and is non-zero. It follows from Proposition 3.1 and the argument above that the number $X = X(n)$ of accessible paths in this case satisfies

$$(3.8) \quad X \gtrsim n! \cdot C_{\eta, \theta}^{n-1},$$

The point is that $C_{\eta, \theta} \in (0, 1]$ is a constant depending only on η and θ .

ACKNOWLEDGEMENTS

We thank Joachim Krug for making us aware of the problems studied here, and both he and Stefan Nowak for helpful discussions.

REFERENCES

- [A] T. Aita, H. Uchiyama, T. Inaoka, M. Nakajima, T. Kokubo and Y. Husimi, *Analysis of a local fitness landscape with a model of the rough Mt. Fuji-type landscape: application to prolyl endopeptidase and thermolysin*, Biopolymers **54** (2000), No.1, 64–79.
- [AS] N. Alon and J. Spencer, *The Probabilistic Method (2nd edition)*, Wiley (2000).
- [CH] M. Carneiro and D.L. Hartl, *Adaptive landscapes and protein evolution*, Proc. Natl. Acad. Sci. U.S.A. **107** (2010), 1747–1751.
- [Co1] L. Comtet, *Sur les coefficients de l'inverse de la série formelle $\sum n!t^n$* (French), C. R. Acad. Sci. Paris Sér. A-B **275** (1972), A569–A572.
- [Co2] L. Comtet, *Advanced Combinatorics: The Art of Finite and Infinite Expansions*, Reidel, Dordrecht (1974).
- [FKVK] J. Franke, A. Klözer, J.A.G.M. de Visser and J. Krug, *Evolutionary accessibility of mutational pathways*, PLoS Comput. Biol. **7** (2011), No.8, e1002134, 9pp.
- [FWK] J. Franke, G. Wergen and J. Krug, *Records and sequences of records from random variables with a linear trend*, J. Stat. Mech. Theory Exp. (2010), No.10, P10013, 21pp.
- [KL] S. Kauffman and S. Levin, *Towards a general theory of adaptive walks on rugged landscapes*, J. Theoret. Biol. **128** (1987), No.1, 11–45.
- [Ki] J.F.C. Kingman, *A simple model for the balance between selection and mutation*, J. Appl. Probability **15** (1978), No.1, 1–12.
- [Klo] A. Klözer, *NK Fitness Landscapes*, Diplomarbeit Universität zu Köln (2008).
- [O1] The Online Encyclopedia of Integer Sequences, Sequence #A003319. <http://oeis.org/A003319>
- [O2] The Online Encyclopedia of Integer Sequences, Sequence #A059438. <http://oeis.org/A059438>
- [W1] D.M. Weinreich, N.F. Delaney, M.A. DePristo and D.M. Hartl, *Darwinian evolution can follow only very few mutational paths to fitter proteins*, Science **312** (2006), 111–114.
- [W2] D.M. Weinreich, R.A. Watson and L. Chao, *Perspective: Sign epistasis and genetic constraints on evolutionary trajectories*, Evolution **59** (2005), No.6, 1165–1174.

DEPARTMENT OF MATHEMATICAL SCIENCES, CHALMERS UNIVERSITY OF TECHNOLOGY AND UNIVERSITY OF GOTHENBURG, 41296 GOTHENBURG, SWEDEN
E-mail address: `hegarty@chalmers.se`

DEPARTMENT OF MATHEMATICAL SCIENCES, CHALMERS UNIVERSITY OF TECHNOLOGY AND UNIVERSITY OF GOTHENBURG, 41296 GOTHENBURG, SWEDEN
E-mail address: `andemar@chalmers.se`